

Supplementary Material

I. Formal correspondence of alternative models of spike threshold

In modeling the relationship between V_1/V_0 and R_1/R_0 , several models of the spike-rate generator are possible. The most general is a 3-parameter model:

$$R(V) = k(V - V_{th})^p, \quad V > V_{th}, \quad k > 0 \quad p > 0$$

$$R(V) = 0, \quad V \leq V_{th}$$

Eq. S 1.

Where R is spike rate, V is the membrane potential, p is an exponent and k is a gain factor, and V_{th} is a threshold voltage. V_{th} is not the biophysical threshold, but is instead a free parameter determined in the fitting procedure. In the paper, we have assumed that V_{th} is equal to V_{rest} yielding a 2-parameter model. With p set to 1, the model becomes the familiar threshold-linear model of spiking, which was used by Mechler and Ringach in their original formulation of the transformation between R_1/R_0 and V_1/V_0 . As we showed in the paper for the power-law model, we will demonstrate here that the threshold-linear model of spiking predicts a bimodal distribution of R_1/R_0 from the measured distribution of V_1/V_0 .

For modeling the transformation, we assume (Figure S1.b) that when the neuron is stimulated by a sine grating, the membrane potential, $V(t)$, is sinusoidally modulated in time at the grating frequency, f :

The contribution of spike threshold to the dichotomy of cortical simple and complex cells

Nicholas Priebe, Ferenc Mechler, Matteo Carandini, and David Ferster

$$V(t) = V_0 + V_1 \cos(2\pi ft)$$

Eq. S 2,

where V_0 is the stimulus-induced mean elevation of the potential above the resting level (the nonlinear response component), and V_1 is the amplitude of the stimulus-induced sinusoidal modulation of the voltage (the linear component). With these assumptions, the threshold model associated with a fixed exponent, p , predicts¹ that the R_1/R_0 firing rate modulation ratio is a nonlinear function, \mathbf{g} , of a single variable, χ .

$$\begin{aligned}\chi &= (V_{th} - V_0) / V_1 \\ R_1 / R_0 &= g_p(\chi)\end{aligned}$$

Eq. S 3,

Figure S1.c shows this nonlinear function for two fixed exponents, $p=1$ and $p=2$. The analytic form of $\mathbf{g}_p(\chi)$ exists¹ for cosine modulation and for all positive real p exponents of the threshold nonlinearity. $\mathbf{g}_p(\chi)$ behaves as a nonlinear ruler. \mathbf{g} does not depend on the gain parameter, k , because k appears in both the numerator and the denominator of the variable, χ . For all choices of the parameter, p , \mathbf{g} has a sigmoid shape. This sigmoid shape is also preserved when the cosine shape of the modulation potential waveform is distorted by noise.

For depolarizing membrane potential responses ($V_0 \geq 0$), nonlinear transformation between χ and R_1/R_0 can be reformulated into the relationship between V_1/V_0 and R_1/R_0 as follows:

$$\begin{aligned}\chi &= V_{th} / V_1 - V_0 / V_1 = a - 1 / (V_1 / V_0) \\ R_1 / R_0 &= g_p(a - 1 / (V_1 / V_0)) = G_{p,a}(V_1 / V_0)\end{aligned}$$

Eq. S 4,

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where, $\mathbf{G}_{p,a}(V_1/V_0)$ is a family of continuous elbow-shaped functions parametric in the exponent p and the parameter $a = V_{th}/V_1$. $\mathbf{G}_{p,0}(V_1/V_0)$ is the subset of functions that are parametric only in the exponent and correspond to 2-parameter power-law models considered in the paper ($V_{th} = V_{rest} = 0$). Figure S1.d shows $\mathbf{G}_{1,0}(V_1/V_0)$ and $\mathbf{G}_{2,0}(V_1/V_0)$; the three examples shown in the main text of the paper were for exponents $p = \{2, 3, 5\}$. The responses defined by Eq. S4 correspond to responses in Eq. S3 with the constraint that $V_0 > 0$ (that is, $\chi_0 \leq 0$). Note also that an entire family of functions, $\mathbf{G}_{p,a}(V_1/V_0)$ with a fixed p but varying in threshold (as quantified by the parameter, a), corresponds to the single sigmoid $\mathbf{g}_p(\chi)$, again subject to the $V_0 > 0$ constraint.

This change of models from R_1/R_0 as a function of χ to R_1/R_0 as a function of V_1/V_0 makes the nonlinear transformation easier to interpret because it recasts the problem as a mapping between the two quantities that are directly measured. Because the power-law models require that V_0 be greater than 0, the maximum amount of spike-rate rectification that can occur is half-wave. Therefore, to account for large firing rate modulation ratios ($R_1/R_0 \approx 2$), the power law models require large exponents. Thus, the threshold parameter in the threshold-linear model plays a similar role as the exponent in the power-law models: higher threshold voltage in the first has the same effect as larger exponents in the second. Compare members of the $\mathbf{G}_{1,a}(V_1/V_0)$ function family corresponding to parameter $a = \{0, 0.2, 0.5, 1, 1.5\}$ shown in Figure S1.e with members of the $\mathbf{G}_{p,0}(V_1/V_0)$ family corresponding to parameter $p = \{0.5, 1, 2, 4, 8\}$ shown in Figure S1.f. Increasing line thickness indicates increasing parameter values in both figures.

Supplementary Material

II. Testing the threshold-linear model

In the paper, we demonstrated that the power-law model fit the transformation between V_1/V_0 and R_1/R_0 reasonably well. We now show that a threshold-linear model can also account for most of the variance in the R_1/R_0 data. As for the power law model, we fit the threshold-linear model to the relationship between membrane potential and firing rate for each neuron using V_{th} and k ($p=1$). Figure S2.a shows the relationship between the fitted parameter, V_{th} , and the measured action potential threshold. Notice that the fitted thresholds are systematically smaller than the measured thresholds. The difference in the values arises because voltage noise acts to randomly bring the membrane potential to action potential threshold². In the power-law model, voltage noise is accounted for by the exponent, p ³.

The distribution of the intracellular ratio, $\chi = (V_{th} - V_0)/V_1$, is unimodal in our population of V1 neurons (Figure S2.b), as would be expected from the observation that V_1 , V_0 and V_{th} are unimodally distributed. For reference, the bimodal distribution of R_1/R_0 is re-plotted in Figure S2.c. The transformation of χ into R_1/R_0 is nonlinear (Figure S2.d; one data point for each neuron). Consistent with the assumption of the threshold-linear model, the 95% confidence interval of the fit exponent overlapped 1 for the population of V1 neurons ($p = 0.78 \pm 0.39$). The threshold-linear model accounted for 78% of the variance in the relationship between χ and R_1/R_0 . The prediction of spike modulation ratio by the threshold-linear model is therefore only slightly weaker (Figure S2.e) than the prediction by the power-law model (Figure 3D, main text).

The contribution of spike threshold to the dichotomy of cortical simple and complex cells

Nicholas Priebe, Ferenc Mechler, Matteo Carandini, and David Ferster

The scatter about the optimal sigmoid can be explained by a combination of neuronal noise, error from the choice of model or nonsinusoidal shape of the voltage response. Some of the systematic deviations from the threshold-linear model could be accommodated by a diversity of exponents. Systematic distortions to the cosine shape, such as broadened or narrowed peaks and troughs, are often observed in intracellular recordings of V1 neurons' responses to sine gratings. The model can accommodate such distortions by using a class of functions other than the cosine (e.g., von Mises functions) with appropriately redefined amplitude and mean¹.

References

1. Mechler, F. & Ringach, D. L. On the classification of simple and complex cells. *Vision Res* **42**, 1017-33 (2002).
2. Carandini, M. & Ferster, D. Membrane potential and firing rate in cat primary visual cortex. *J Neurosci* **20**, 470-84 (2000).
3. Anderson, J. S., Lampl, I., Gillespie, D. C. & Ferster, D. The contribution of noise to contrast invariance of orientation tuning in cat visual cortex. *Science* **290**, 1968-72. (2000).

Supplementary Figure Legends

Figure S1.

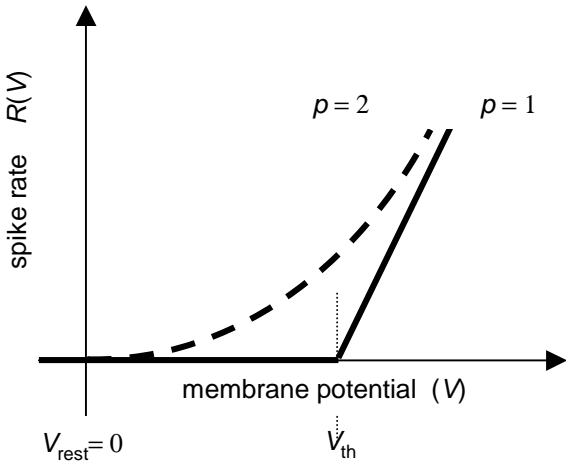
Comparison of alternative threshold models. **(a)** The static nonlinearity of threshold is modeled by a power function that converts the supra-threshold potential input into firing rate output. The two examples shown are the threshold-linear model ($p = 1, V_{\text{rest}} < V_{\text{th}}$), indicated by the continuous curve, and the power-law model ($p = 2, V_{\text{th}} = V_{\text{rest}}$), indicated by dashed curve. **(b)** The synaptic response to a drifting grating is modeled by a sinusoidal modulation of the membrane potential. For definition of quantities, see text of Supplementary Material I. **(c)** $\mathbf{g}_p(\chi)$, the sigmoid mapping of the intracellular ratio, χ , into R_1/R_0 , the spiking modulation ratio. The two examples shown correspond to exponents $p = 1$ (continuous curve) and $p = 2$ (dashed curve). V_{th} is a free parameter in both. **(d)** $\mathbf{G}_{p,0}(V_1/V_0)$, the elbow shaped mapping of V_1/V_0 , the intracellular modulation ratio into R_1/R_0 . The two examples shown correspond to exponents $p = 1$ (continuous curve) and $p = 2$ (dashed curve). $V_{\text{th}} = V_{\text{rest}}$ in both. **(e)** $\mathbf{G}_{1,a}(V_1/V_0)$, shown for $a = \{0, 0.2, 0.5, 1, 1.5\}$ by curves of increasing thickness. **(f)** $\mathbf{G}_{p,0}(V_1/V_0)$, shown for $p = \{0.5, 1, 2, 4, 8\}$ by curves of increasing thickness.

Figure S2.

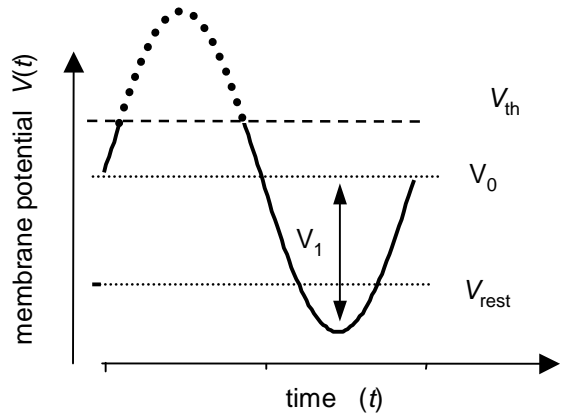
Evaluation of the threshold-linear model. The gain and threshold parameters were optimized for each V1 neuron as in the main text of the paper. Cell types are indicated by color; simple cells by red, complex cells by black. **(a)** Scatter plot of the fit parameter V_{th} and the measured action potential threshold. **(b)** Unimodal distribution of the intracellular ratio $\chi = (V_{th} - V_0)/V_1$. **(c)** Bimodal distribution of R_1/R_0 , the spiking modulation ratio. **(d)** Transformation of χ to R_1/R_0 . The thin black indicate $g_p(\chi)$, that correspond (from bottom up) to exponents $p = \{0.5, 1, 2\}$. The thick blue curve indicates the sigmoid $g_p(\chi)$ that optimally accounts for the data. The optimal exponent, $p=0.78$, is not significantly different from 1. **(e)** Using the threshold-linear model the correlation between predicted and measured R_1/R_0 is slightly weaker ($R^2 = 0.56$) than when the power-law model was used (Fig 3D, main paper). The linear regression (blue dashed line) is significantly different from identity (black solid line) (slope = 0.62; $p < 0.01$; y-intercept = 0.27, $p < 0.01$).

Figure S1

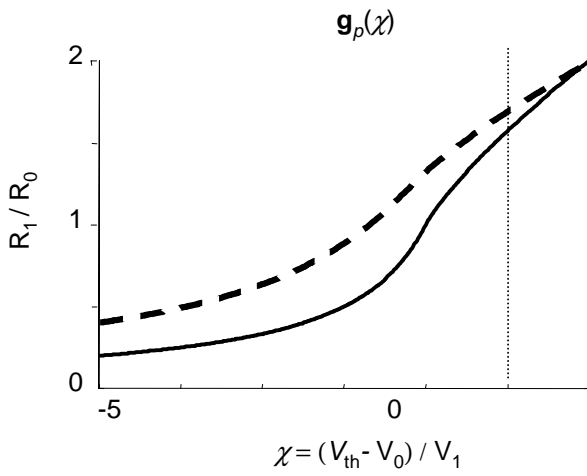
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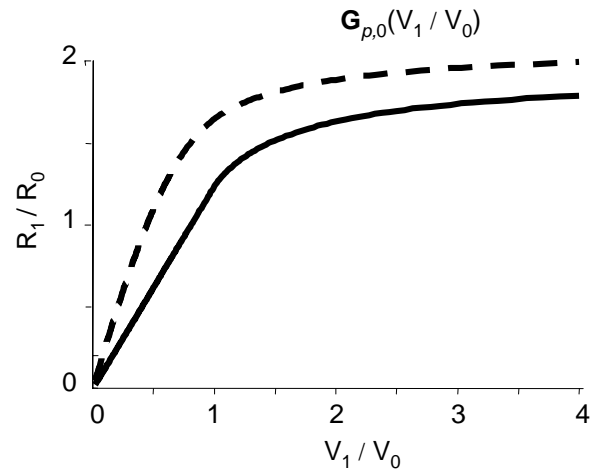
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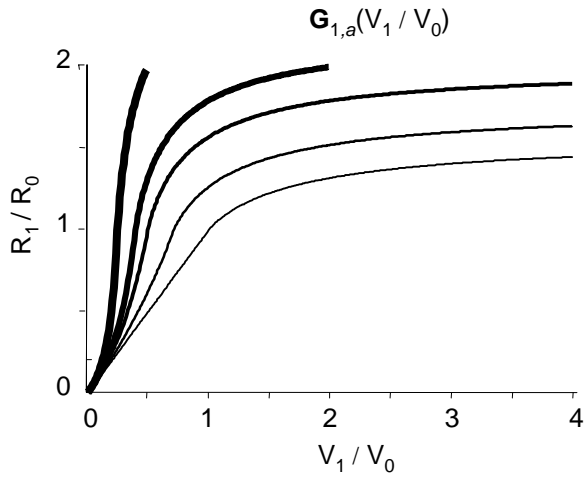
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e



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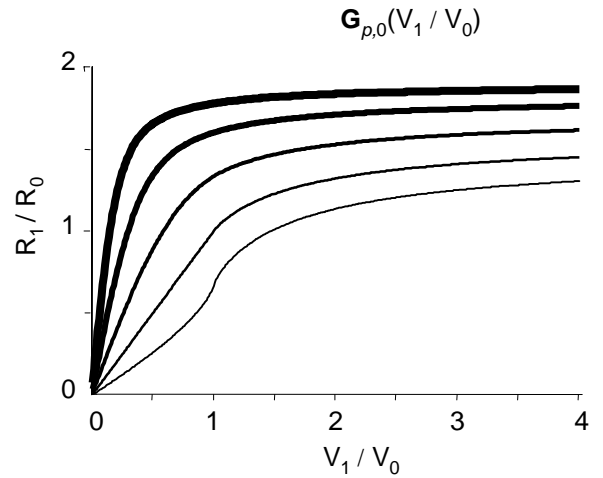


Figure S2

